REVIEW *New Phytol.* (2000), **147**, 55–71

Research review

Spatial and temporal deployment of crop roots in CO_2-enriched environments

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Received 4 November 1999; accepted 7 March 2000

SUMMARY

Growth of crops in CO_2-enriched atmospheres typically results in significant changes in root growth and development. Increased root carbohydrates stimulate root growth either directly (functioning as substrates) or indirectly (functioning as signal molecules) by enhancing cell division or cell expansion, or both. Although highly variable, the literature suggests that, generally, initiation and stimulation of lateral roots is favored over the elongation of primary roots, leading to more highly branched, shallower root systems. Such architectural shifts can render root systems less efficient, perhaps contributing to the lower specific root activities often reported. Allocation of carbon (C) to roots fluctuates through the life of the plant; root functional and growth responses should therefore not be viewed as static. In annual crops, C allocation to belowground processes changes as vegetative growth switches to reproduction and maturation. Reductions in C allocation to roots over time might cause temporal shifts in root deployment, perhaps affecting root demography. However, significant changes in root turnover (defined here as root flux or mortality relative to total root pool size) as a result of decreased root longevities in crop plants are unlikely. Consideration of changing C allocation to roots, a more thorough understanding of the mechanistic controls on root longevity, and a better characterization of the rooting habits (life histories) of different crop species will further our understanding of how increasing atmospheric [CO_2] will affect root demography. This knowledge will lead the way toward a more thorough understanding of the linkage of atmosphere with belowground plant function and also that of plant function with soil biology and structure. Ultimately, successful modeling of global C and nitrogen (N) cycles will require empirical data concerning spatial and temporal deployment of roots for a range of crop species grown under different agricultural management systems.

Key words: roots, elevated [CO_2], root turnover, root demography, root development, carbon allocation.

INTRODUCTION

Exposure of crop species to elevated atmospheric [CO_2] often results in large shifts in root structure and function (Berntson & Woodward, 1992; Ferris & Taylor, 1994). Several reviews focusing on belowground plant responses to increasing atmospheric [CO_2] have been published in the past decade, and it is now becoming clear that roots often achieve the greatest and most consistent growth enhancement of all plant parts when grown with elevated [CO_2] (Rogers *et al.*, 1994; Batts *et al.*, 1998). However, our understanding of root responses is limited because most data that address the responses of crop roots to global change point to shifts in total root biomass or to changes in root structural characteristics at only a single sampling period (Norby, 1994; Rogers *et al.*, 1994, 1996, 1997, 1999). Examination of rooting characteristics (structure and function) at a single point in time can be confounded by 'ontogenetic drift', resulting in misleading conclusions about C allocation patterns (Stulen & den Hertog, 1993; Norby, 1994; Fitter *et al.*, 1996, 1997). For example, there might be transient, short-lived changes in allocation patterns of photosynthate resulting in permanent alterations in the proportion of biomass in aboveground in comparison with belowground structures, which a single sampling would not reflect. Few studies have examined how more dynamic patterns of root deployment (in time and space) and function might be affected (Norby,

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1994). Clearly, a more complete understanding of how increasing [CO_2] will affect plant and soil C and N dynamics will require that investigators go beyond reporting static measures of the biomass of roots added to the soil C pool.

The objectives of this paper are to express the importance of understanding the dynamic aspects of rooting characteristics in crop species and to review current knowledge about how rising atmospheric [CO_2] might affect root processes. We shall focus on how root initiation, development, and longevity is (or might be) altered by growth in CO_2-enriched atmospheres so as to improve our understanding of how temporal and spatial patterns of root deployment will be affected.

ROOT MERISTEM FUNCTION

Plant root development is the consequence of root meristem function. Root growth is driven by cell division, expansion and differentiation (Taylor, 1997). It follows that the larger root systems of plants grown in CO_2-enriched environments must result either from more and/or larger cells. Understanding the mechanistic basis underlying enhanced cell expansion and cell division in plants grown with CO_2 enrichment will enable us to understand the interface of environmental conditions, endogenous C and N pools, gene expression, and growth and development. Specifically, linking environmental conditions with patterns of hormone, carbohydrate, and N flux to and from active meristems, and understanding how this flux impinges upon and mediates fundamental growth processes, will permit us to understand better how C allocation drives growth. Pritchard *et al*. (1999) presented a conceptual model that illustrates the channels through which increased atmospheric CO_2 availability might affect aboveground and belowground plant structure. They stressed that, to be able to predict changes in whole-plant growth, one must understand how new cells are born, enlarge, and differentiate.

Cell division

The factors that regulate cell division and expansion have recently been discussed in a general sense (Cosgrove, 1993, 1997; Jacobs, 1997) and also in the context of increasing atmospheric [CO_2] (Ferris & Taylor, 1994; Taylor *et al*., 1994; Pritchard *et al*., 1999). We need to understand the relative contributions of increased cell division and enhanced cell expansion in stimulating root system growth in CO_2-enriched atmospheres (Ferris & Taylor, 1994; Taylor *et al*., 1995; Crookshanks *et al*., 1998). Kinsman *et al*. (1997) reported that increased root growth in *Dactylis glomerata* resulted from a greater proportion of dividing cells in the apical meristem. They also observed greater mitotic indices indicative of shortened cell cycles. They attributed increased root growth to a stimulation in cell division, perhaps resulting from greater carbohydrate availability.

One key to understanding how root growth (and shoot growth) will change in a high-[CO_2] environment lies in an understanding of how carbohydrates, especially sucrose, function both as substrates for growth and as regulatory molecules. Increased sucrose transported to active root meristems might have direct (functioning as a substrate for growth) and indirect (functioning as a plant growth regulator) effects on cell division (Francis, 1992; Williams *et al*., 1992). Williams *et al*. (1992) showed that experimentally manipulating the balance of sucrose between sources and sinks induces changes in metabolism and patterns of protein synthesis in both roots and shoots. They suggested that sucrose might function as a plant growth regulator in a fashion similar to that described for hormones. For example, sucrose might have a role as a chemical control point in the cell division cycle (Francis, 1992; Ranasinghe & Taylor, 1996), perhaps acting by mediating cyclin activity (Kinsman *et al*., 1997). Cyclins, a class of regulatory subunits of a family of protein kinases, have recently been shown to facilitate the transition of cells from G0 to G1 of the cell cycle, thus stimulating division (Soni *et al*., 1995; Jacobs 1997). Doerner *et al*. (1996) suggest that control of cyclin concentrations might allow plants flexible growth control in response to changes in the environment such as nutrient availability. In view of the significant belowground effects of elevated [CO_2] in stimulating total root length and biomass and the often-reported increases in non-structural carbohydrate contents in root tissue, the possible link between root carbohydrate contents and stimulation of cell division merits further study.

Cell expansion

Increased cell expansion resulting in larger root cells could also contribute to increased root growth in elevated [CO_2]. For example, Ferris & Taylor (1994) reported increased root extension rates in *Sanguisorba minor*, *Lotus corniculatus*, *Anthyllis vulneraria*, and *Plantago media* grown in elevated [CO_2]. Cell length was unaffected by CO_2 treatment from *c*. 15–25 μm up to *c*. 1 mm behind the growing root tip. Beyond 1 mm, however, cell length increased at a greater rate in all four species grown in elevated [CO_2] than in ambient [CO_2]. Further, greater turgor pressure in root cells of plants grown in elevated [CO_2] than in ambient [CO_2] led them to conclude that the enhancement of root growth was the result of increased cell expansion induced by greater cell wall loosening, combined with higher cell turgor pressure, rather than by increased cell division. Crookshanks *et al*. (1998) reported a 40%

greater mean root cortical cell length in elevated [CO_2] than in ambient [CO_2] at a distance of 375 μm from the root tip, which was associated with increased cell wall extensibility. From these data, it seems that both cell production and expansion might contribute to the greater size of roots in plants grown in CO_2-enriched environments.

ROOT ARCHITECTURE

Roots of crop plants originally evolved the ability to adjust functionally and developmentally in response to transient nutrient-rich and moisture-rich microsites characteristic of heterogeneous soils. Both traditional breeding methods and, more recently, genetic engineering are being used to enhance their physiological and phenotypic plasticity. We might therefore expect crop plants to exhibit a higher degree of responsiveness to a changing environment than wild species (Zobel, 1996).

Changes in root architecture and spatial distribution in the soil profile resulting from CO_2 enrichment will probably affect plant function and nutrient cycling. For example, Fitter (1996) hypothesized that herringbone (less branched) rooting patterns might increase root efficiency by increasing uptake per unit root volume. Dichotomous (highly branching) root systems, by contrast, might be less efficient, especially for the uptake of mobile resources, because of overlap between the depletion zones of adjacent branches. Similarly, the morphological changes observed in root systems of plants grown with elevated [CO_2] could facilitate either more or less efficient root architectures. To establish a conceptual understanding or framework in which empirical data can be integrated, it is necessary to discuss briefly how roots grow and what aspects of root development contribute to their architectural plasticity.

Primary roots : determinate or indeterminate?

It is not clear whether roots of most plant species (especially annuals) are determinate or indeterminate. In tissue culture, root meristems undergo pronounced aging and cease growth after a strictly limited period; this phenomenon has also been observed in the field (Caldwell, 1977). Gladish & Rost (1993) showed in pea, cotton, and *Arabidopsis* that primary roots have a defined developmental cycle characterized by an acceleration phase followed by a deceleration phase, terminating in arrest, suggesting that at least the primary roots of these species are determinate. Street *et al.* (1952) showed that the main root axis of excised roots of tomato grown in constantly renewed culture elongated for only a limited period and then ceased activity even while more recently initiated lateral roots continued to grow rapidly. They showed that the root tip can then restart growth if it is excised and put into fresh medium. This suggests that there might be a signal from the more mature regions capable of inhibiting or arresting primary root growth. It is also possible, and there is some evidence to suggest, that there is a controller for cell cycle numbers that 'counts' the number of times initial cells divide in most plants (T. Rost, pers. comm.). In *Azolla* (a pteridophyte), for example, the apical cell is programmed to divide 55 times and then increased root growth can be achieved only by increased cell expansion or increased initiation and growth of laterals. In species that have determinate primary roots, there is a suite of structural and ultrastructural changes that reflect the cessation of root elongation (Webster & MacLeod, 1996). An examination of the influence of elevated [CO_2] on these events has not yet been undertaken. Controlled laboratory experiments designed to elucidate specific mechanisms underlying a response (or a lack of response) of primary roots to elevated [CO_2] could provide valuable clues about how the architecture and function of entire root systems will change.

Lateral roots : key determinates of architectural plasticity

Although there might be a continuum ranging from strictly determinate to indeterminate control over the plasticity of primary root elongation, there seems to be more flexibility in the initiation and development of lateral roots (Charlton, 1996; Webster & MacLeod, 1996; Zobel, 1996; Kerk, 1998). Variation in longitudinal patterning is thought to be the main source of root ability to adapt architecturally to the environment (Kerk, 1998). In fact, according to Smucker (1993), perhaps the most important question about root responses to environmental stress is concerned with how stresses are transduced to response mechanisms, ultimately resulting in the activation of cell cycle genes in pericycle cells. When initials of the pericycle are activated, they divide repeatedly, eventually producing a mound of meristematic cells that organize to form a new root meristem (Smucker, 1993; Kerk, 1998). It is not known what sequence of events triggers the activation of pericycle initials, or why some initials are activated to form new roots while others remain inactive. There is evidence to suggest that local environmental conditions (i.e., soil moisture contents, nutrient availability, and soil physical characteristics) interact with hormonal cues (i.e., auxin), and with carbohydrates (i.e., sucrose) to control lateral root initiation and extension (Huck *et al.*, 1987; Smucker, 1993).

It is therefore likely that initiation and extension of lateral roots (as opposed to extension of primary roots) will be the most common result of plant

growth in CO_2-enriched atmospheres, leading to increased root length near the soil surface and a more horizontal spread of roots. For example, CO_2 enrichment resulted in enhanced root proliferation at shallower soil depths in spring wheat (Van Vuuren *et al.*, 1997), winter wheat (Chaudhuri *et al.*, 1990; Fitter *et al.*, 1996), cotton (Rogers *et al.*, 1992b) and sorghum (Chaudhuri *et al.*, 1986). Del Castillo *et al.* (1989) reported for soybean that, although there was no effect on rates of elongation, there was an increase in the number of actively growing roots (more highly branched). Cruz *et al.* (1997) reported that carob seedlings grown in elevated [CO_2] had more lateral roots and produced shorter and thicker roots (more highly branched). In a free-air CO_2 enrichment (FACE) study with cotton, Rogers *et al.* (1992b) showed that the number, length, and mass of lateral roots were enhanced by CO_2 enrichment. However, although taproot diameter, mass, and volume were enhanced, length was not affected. In contrast to these reports, Rogers *et al.* (1992a) reported a 110% increase in root length of soybean but no change in the number of lateral roots.

As seen from the results already discussed, it is probable that the branching and extension of first-order and higher-order laterals might be favored over the extension of the root system deeper into the soil (see Rogers *et al.*, 1999 for a more thorough review of experimental findings so far). This might suggest that, in future higher-[CO_2] environments, crop roots will be larger, more highly branched (especially at shallow depths), but less efficient in nutrient and water uptake (decreased specific root activity). So, as recently discussed by Berntson & Bazzaz (1996), there might be an increase in the potential of entire root systems to acquire resources because of greater total root length densities, but the efficiency of resource capture might decline.

ROOT FUNCTION

Carbon allocation below ground

Experiments and models predict between 25% and 75% increases in leaf-level rates of photosynthesis and 30–40% increases in net primary productivity of agroecosystems as atmospheric [CO_2] doubles in the next hundred years (Berntson & Bazzaz, 1996; Barrett *et al.*, 1998). In natural systems, finite resource availability might constrain the long-term flux of C into plant and soil systems, but for agricultural systems in which nutrients and water are often less growth-limiting, constraints will be less stringent (Berntson & Bazzaz, 1996; Canadell *et al.*, 1996).

For several crop species, up to 40% of net C fixed is allocated below ground (Gorissen, 1996; Gregory *et al.*, 1996), and the proportion of total plant photosynthate allocated to roots tends to increase in plants growing in elevated [CO_2] (Canadell *et al.*, 1996). For example, Rattray *et al.* (1995) reported that the proportion of ^{14}C translocated below ground almost doubled, from 18% at ambient [CO_2] to 34% under elevated [CO_2]. In several studies, increases in canopy C assimilation have been observed that could not be accounted for in aboveground biomass or in standing root biomass (Fitter *et al.*, 1997; Cheng & Johnson, 1998). This 'missing' C has been hypothesized to be due to increases in root C exudation, root respiration, and/or root turnover.

Carbon allocation to root processes

Carbon translocated below ground can have a number of fates, including: (1) conversion into root biomass; (2) respiration for new growth, ion uptake, and maintenance; (3) re-export to shoots; (4) diversion to symbionts such as mycorrhizae; (5) loss as exudates, or sloughed cells; (6) loss to herbivory; and (7) loss in the process of root turnover (Darrah, 1996). Very little is known about how the extra C translocated belowground is utilized by plants and soil microbes in CO_2-enriched environments and the residence times for that C in the plant–soil system (Cotrufo & Gorissen, 1997). To assess how rising atmospheric [CO_2] will affect nutrient cycling in agricultural systems and to understand how these changes will be linked, both quantitatively and qualitatively, to global C and N cycles, we must first understand when, in what form, and how much C flows into, within, and out of soil C pools.

Recent reviews focusing on the effects of elevated [CO_2] on C allocation (Gregory *et al.*, 1996), root : shoot ratios (Rogers *et al.*, 1996), respiration (Lambers *et al.*, 1996), rhizodeposition (Darrah, 1996), and interactions with root symbionts (Díaz, 1996), provide useful information about the fate of C in the plant–soil system in CO_2-enriched environments. In general, plants growing in elevated [CO_2] allocate a greater percentage of fixed C below ground, often resulting in increased root : shoot and root : total plant mass ratios. There has been much speculation about the effects of elevated [CO_2] on root exudation, but it is still not known whether elevated [CO_2] affects exudation per unit root, or whether specific rates of root exudation remain the same but only total root biomass is changed (Cardon, 1996). Clearly more information on C consumption for root growth, maintenance, and uptake respiration as well as the total amount of C entering the rhizosphere as soluble and insoluble exudates is warranted. Uncertainties regarding the transfer of C to soil via root exudation notwithstanding, still less is known about the transfer of C to soil via fine-root turnover, especially for crops. The periodic replacement of finer root elements might represent an

even greater energy demand than maintenance respiration, exudation, C transfer to symbionts, and belowground predation (Caldwell, 1977; Canadell *et al*., 1996).

Recently, the use of minirhizotrons to measure the dynamics of root initiation, growth, and death, and the C tracers ^{14}C and ^{13}C have proved to be powerful tools for determining not only how much C is transported below ground, but how C is being partitioned between different belowground C pools (Meharg, 1994; Cheng & Johnson, 1998). Swinnen *et al*. (1994) produced a complete C budget for wheat by using ^{14}C pulse labeling. They found that 29% of fixed C was allocated below ground. Of this belowground C pool, 22% was lost as rhizosphere rhizodeposition, 16% was lost as fine-root turnover, 40% was lost as root respiration, and 22% was recovered in live roots at harvest. This study points out the importance of considering all belowground activity; assessing the C allocation to roots would have been largely underestimated if only live roots at harvest had been taken into consideration. It is also important to remember that patterns of C allocation to root systems change with the stage of development in crop plants (Gregory *et al*., 1996). In general, C allocation to root systems is greatest early in the growing season and declines with increasing maturity. Swinnen *et al*. (1994) reported for winter barley that instantaneous C allocation to roots systems changed from 39% at stem elongation to 23% at anthesis, and to 17% at dough ripening. To our knowledge, similar detailed accounting of all belowground C in crops growing in CO_2-enriched atmospheres has not been undertaken.

Nutrient uptake

Physiological activity of roots might be as important for root function as increases in root biomass and shifts in root architecture. Although root biomass is often increased when plants are grown in elevated [CO_2], there is little evidence to suggest up-regulation in root physiology (Jackson & Reynolds, 1996). In fact, root specific activity is often down-regulated in crop plants grown in elevated [CO_2], despite the fact that roots often have greater quantities of nonstructural carbohydrates present in root tissue (Jongen *et al*., 1995; BassiriRad *et al*., 1996) and the fact that nutrients are often supplied at nonlimiting levels (Newbery *et al*., 1995; Hodge *et al*., 1998). Lower specific rates of root activity are reflected by greater C : nutrient ratios in conjunction with decreased tissue concentrations of nutrients including N (Israel *et al*., 1990; Hodge *et al*., 1998) and potassium (K; Newbery *et al*., 1995). Decreases in nutrient uptake efficiency might result from the production of more inefficient root architectures (Fitter, 1996), from limitations imposed by anatomical characteristics (Bunce, 1996; Huxman *et al*., 1999), from reduced mass flow of water through the soil–plant–air continuum (Lambers *et al*., 1996), from inefficient or unbalanced plant C and N relations, or from a reduction in the competitive ability of roots (in comparison with microbes and the roots of competing plants) to acquire nutrients (Díaz *et al*., 1993).

However, decreased nutrient concentrations in plants grown with CO_2 enrichment do not necessarily indicate reductions in specific rates of nutrient uptake. As recently discussed by Stitt & Krapp (1999), reductions in nutrient concentrations have been interpreted differently. Decreased nutrient concentrations might result from soil-nutrient limitations that sometimes plague pot studies (McConnaughay *et al*., 1993), from higher nutrient use efficiencies (Rogers *et al*., 1997, 1999), or from dilution of nutrients by the accumulation of total nonstructural carbohydrates (TNC) (Kuehny *et al*., 1991). However, decreased nutrient concentrations often persist even when TNC are subtracted. For example, Poorter *et al*. (1997) examined the chemical composition of 27 well fertilized plants representing crop, wild herbaceous, and woody species. They found that mineral concentrations were consistently reduced in plants grown with CO_2 enrichment even when expressed on a TNC-free basis. Because plants sampled in this experiment were grown at a number of different laboratories, these results should provide a good estimate of response patterns for well nourished plants growing in high [CO_2] (Poorter *et al*., 1997). Kuehny *et al*. (1991) also found that decreases in Fe, Mn, Zn, and Cu concentrations in high-[CO_2]-grown *Chrysanthemum* were still significant when starch was subtracted out. From these data it seems that reduced specific rates of nutrient uptake cannot be ruled out as an explanation for lower plant-nutrient concentrations induced by exposure to elevated atmospheric [CO_2].

Growth in elevated [CO_2] might have differential effects on the uptake efficiency of different nutrients or different chemical forms of the same nutrient. Such differential effects of elevated [CO_2] on the uptake of different nutrients might contribute to inconsistent reports in the literature about the impact of elevated [CO_2] on specific root activity. Jackson & Reynolds (1996) found that physiological rates of ammonium uptake were unchanged in six grass species with elevated [CO_2], but rates of nitrate uptake decreased. Van Vuuren *et al*. (1997) showed that elevated [CO_2] affected the uptake of different nutrients in different ways: K uptake declined while P uptake increased. They suggest that the uptake of highly immobile elements such as P and Zn might be enhanced because of more thorough soil exploration owing to increased root length density. Conversely, the uptake of highly diffusable nutrients such as N might be reduced because of increased water use

efficiency resulting in a reduced mass flow of nutrients in the transpiration stream (Lambers *et al.*, 1996).

Respiration and hydraulic conductivity

Respiration of plants is generally inhibited by growth in elevated [CO_2] (Gifford *et al.*, 1985; BassiriRad *et al.*, 1996; Fonseca *et al.*, 1996; Fitter *et al.*, 1997; but also see Lambers *et al.*, 1996), even when nutrients are provided at nonlimiting levels. In general, rates of ATP production (a function of respiration rates) are linearly related to the fresh weight of the root and increase with concentrations of tissue N, protein, and carbohydrate (van der Westhuizen & Cramer, 1998). Because root fresh weights and carbohydrate contents are typically enhanced, reductions in respiration might result from decreased nutrient uptake efficiency. An excellent discussion on the effects of elevated [CO_2] on mitochondrial respiration has been published recently (Drake *et al.*, 1999).

Other changes in root function have been reported in crop plants grown with elevated [CO_2]. In a study of wheat plants grown with elevated [CO_2], Barrett *et al.* (1998) reported that phosphatase activity of roots was increased owing to an increased amount or activation of enzyme per cell rather than changes in root morphology. Extracellular phosphatases hydrolyse the ester bonds of organic P compounds and their up-regulation is typically associated with limitations in P. Further work on potential biochemical and molecular compensatory responses of roots resulting in the up-regulation of nutrient uptake potential is warranted. Decreases in hydraulic conductivity of soybean roots and *Helianthus* roots have been reported (Bunce, 1996; Huxman *et al.*, 1999). The authors speculated that these decreases were attributable to changes in root morphology or anatomy.

Root response to CO_2 enrichment : a transient response?

Growth enhancement of roots of plants grown in elevated [CO_2] might be a transient response of the plant, similar to that discussed for the stimulation of leaf level photosynthesis and growth enhancement of shoots. However, we are not aware of any study that has attempted to compare the synchrony of root and shoot growth of crop species in CO_2-enriched environments. Fonseca *et al.* (1997) reported that *Plantago major* exhibited an increase in RGR on exposure to CO_2-enriched environments for the first week of the experiment. After 1 wk, however, RGR returned to control (ambient [CO_2]) levels. The transient increase in RGR was accompanied by a transient 40% increase in N metabolism (increased nitrate reductase activity), a 23% increase in root soluble sugar concentration and a 21% increase in root respiration. After RGR had returned to control levels (approx. 8 d), soluble sugar concentrations and root respiration rates returned to control levels, and nitrate reductase activity was actually lowered in roots from plants grown in elevated [CO_2]. Even though elevated [CO_2] stimulated RGR for only 1 wk, the total fresh weight of plants was 30% higher at the end of the experiment. There might be temporary changes in C allocation to roots that result in a net difference in root fraction throughout the experiment (Stulen & den Hertog, 1993; Norby, 1994; Fitter *et al.*, 1996; Van Noordwijk *et al.*, 1998). That is, changes in total belowground biomass at the end of the experiment do not necessarily represent a continued increase in input to the belowground C pool. As C allocation to roots changes through time, root functional shifts also occur. To understand root metabolic responses to elevated [CO_2], function must be viewed as a dynamic process.

This inability of plants to acquire enough nutrients to accommodate increased C assimilation introduces a nutrient dimension to the often-discussed compromise between plant water loss and C assimilation. Exposure to elevated [CO_2] increases photosynthesis, resulting in greater C transport to roots. However, stomatal conductance and transpiration per unit leaf area also decrease, which reduces the passage of mobile nutrients into the plant through the transpiration stream. So, even when supplies of nutrients are freely and continuously available to roots, their uptake does not always increase proportionally with growth and thus nutrient concentrations in tissues can decrease (Newbery *et al.*, 1995). The inability of plants to acquire more nutrients to compensate for additional C, in some species, might act as a negative feedback to enhanced growth at elevated [CO_2]. This compromise might even prevent crop plants from realizing the full potential benefit of greater atmospheric C availability.

ROOT TURNOVER IN CROPS

Costs and benefits of root turnover

Fine roots, representing perhaps the principal pathway for the absorption of nutrients and water, undergo periodic replacement (Eissenstat, 1992). The replacement of older roots with newly formed roots is commonly referred to as root turnover. Root turnover, for the purposes of this review, is defined as the absolute rate of root death (or flux) divided by the absolute root pool size. Root turnover represents an important energy consideration to the plant. Caldwell (1977) suggested that at least 25% of root systems die and are replaced annually, accounting for as much as 50–80% of net production for a variety of perennial plant systems. The death of

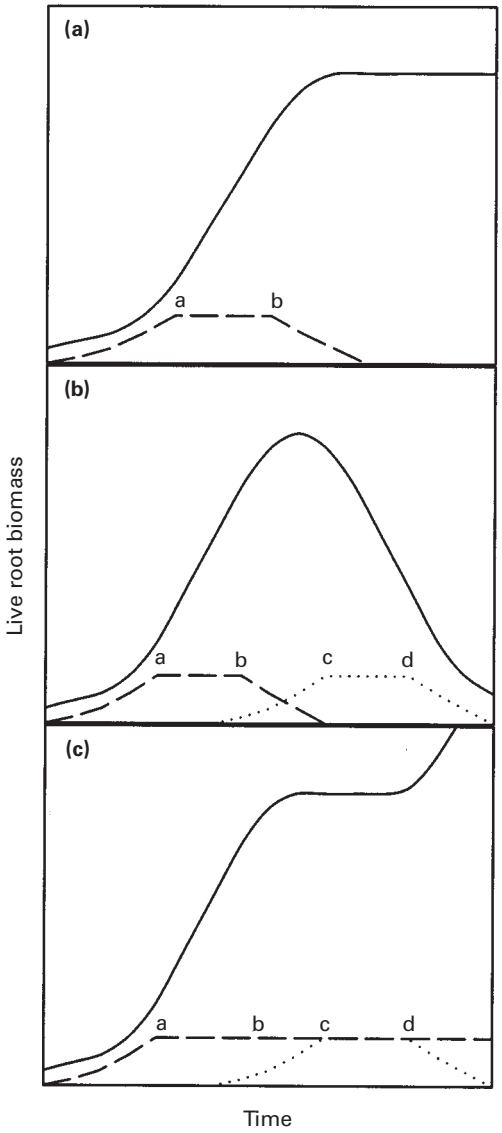

Fig. 1. Theoretical patterns of rooting habits proposed by Huck *et al.* (1987). (a) Species that exhibit no root death and normal root growth. Root density is controlled by root growth processes only. (b) Species exhibiting both normal growth and normal death. Standing live root density represents a balance of production and mortality. (c) Species with continuous growth and normal death. Population curves are solid; growth curves are broken; death curves (in b and c) are dotted. See 'Life history of root longevity' for further details. Figure reprinted from Huck *et al.* (1987) with permission from the American Society of Agronomy.

older fine roots and the construction of new ones represents a considerable energetic cost to the plant. Understanding the trade-offs between the cost of maintaining old roots compared with that of building new ones is an important first step in understanding how increased C assimilation, associated with rising global [CO_2], will affect root turnover. Van Noordwijk *et al.* (1998) recently presented an excellent quantitative discussion of these trade-offs. They calculated that, for a root with a growth respiration of 2 g CH_2O g^{-1} root d. wt and a maintenance respiration of 0.03 g C g^{-1} root d. wt d^{-1}, approx. 60 d of root maintenance in unfavorable conditions would cost as much as one cycle of root death followed by regrowth. Van der Werf *et al.* (1988) showed, for a different species, that the ATP costs of producing 1 g f. wt of root is approximately equal to the cost of maintaining 1 g of root for 10 d. It might therefore actually be more energetically expensive to maintain fine roots when the costs of maintenance during periods of stress exceed the costs of constructing new roots upon the return of more favorable soil conditions.

Experimental work lends support to this theoretical 'cost–benefit' explanation for root turnover. For example, the death of fine roots and the construction of new roots have been shown to correspond to the availability of soil water and nutrients (Huck *et al.*, 1987; Smucker, 1993). Huck *et al.* (1987) found that root birth and death rates were mediated in time by rainfall events and were mediated in space by the presence of moist soil microsites. They observed that the number of active soybean roots decreased after each rain, increased rapidly during dry periods, then declined again after another rainfall. They also found that spatial peaks in root construction during dry conditions occurred in the soil profile where the most moisture was available.

It is difficult to speculate about how increased C assimilation associated with elevated [CO_2] will affect the trade-off between maintaining old roots and building new ones. Van Noordwijk *et al.* (1998) hypothesized that increasing atmospheric [CO_2] is not likely to exert a significant direct effect (one resulting from a greater C supply) on root turnover. However, indirect effects, mediated by shifts in plant water and nutrient relations, are likely. Experimental evidence shows that root turnover increases more often than not (Pregitzer *et al.*, 1995; Canadell *et al.*, 1996). Canadell *et al.* (1996) summarized several studies in which root turnover was measured. In four experiments with grass systems, increased root turnover occurred in three, and in one did not change. In four experiments on trees, increased turnover was observed in three, while one showed a decrease. Finally, no difference in root turnover was observed in wheat grown in elevated [CO_2] (Fitter *et al.*, 1996). Although still speculative, it is likely that root turnover will be affected differently in annual plants and in perennial plants. This idea deserves study.

Life history of root longevity

Fine-root demographics of different crop species might have a definable pattern that parallels, or is at least integrated with, aboveground life cycle events. Clearly, fine roots of perennial and annual crop species show considerable plasticity in controlling production and mortality depending on both aerial

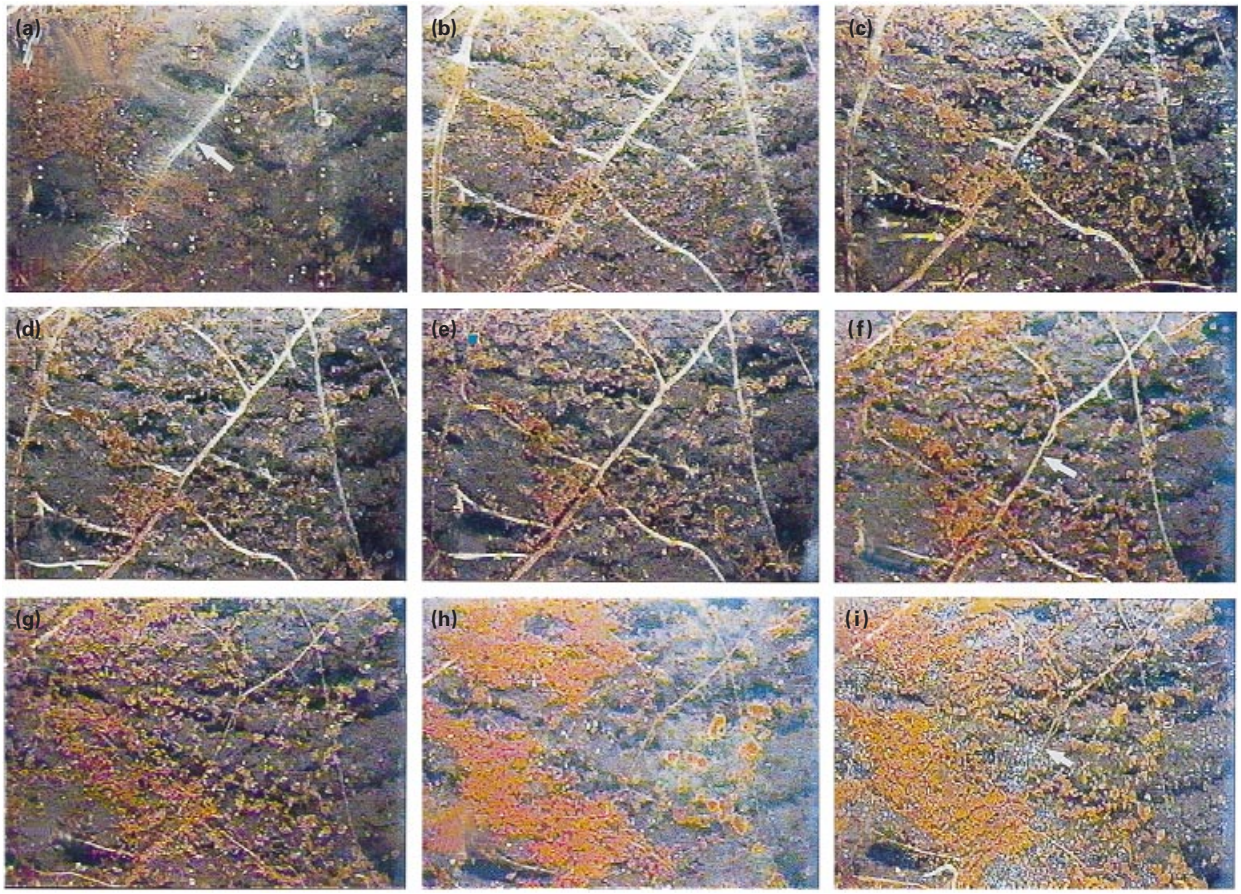

Fig. 2. Sequence of minirhizotron images of winter wheat collected nine times during the growing season. Each frame represents an area of soil 18 mm × 13.5 mm. (a) 14 d after planting (dap). Note the large root growing through the image (arrowed); root hairs are clearly visible. (b) 39 dap; root hairs are still visible. (c) 67 dap; root hairs are no longer visible. (d) 87 dap; (e) 108 dap; (f) 122 dap; the diameter of the root is beginning to decrease, presumably as a result of cortex sloughing. (g) 140 dap; root cortex regions have sloughed off, leaving only a thin strand of vascular tissue. According to Deacon (1987), sloughing of the cortex of wheat roots (programmed cell death) represents a normal ageing process typical of some cereals. Vascular tissue left behind might be functional (Deacon, 1987). (h) 160 dap; (i) 175 dap. Notice that the root marked in (a) is still present (arrowed), but with a reduced diameter. Wheat roots typically exhibit rooting habits consistent with Fig. 1a (with little root death until the end of the life cycle). The use of minirhizotron sequences, as illustrated here, is providing important information about root hair longevity, temporal dynamics of cortex sloughing, and root demography as affected by changing global environments.

and edaphic environmental conditions. Although we are just beginning to understand how root demography is affected by environmental conditions, we are even further from understanding how rooting habits might differ between functional plant groups. Just as different plants have different ways of deploying aboveground biomass (annual vs perennial, deciduous vs evergreen leaves) they also have different strategies for deploying belowground biomass (life history strategies; Eissenstat & Yanai, 1997).

The strategies of fine-root deployment adopted by annual and perennial crops might differ considerably. Annual plants have only one growing season in which to grow and maintain all the roots necessary for the uptake of sufficient water and nutrients for reproduction. By contrast, perennial root systems can exhibit a wider range of life history strategies because they are not constrained by a single growing season. Fig. 1 (Huck *et al.*, 1987) illustrates three theoretical patterns of root production and mortality. This figure is instructive for formulating hypotheses about how elevated [CO_2] might affect root demography. Fig. 1a represents a pattern with no root death involving a period of increasing growth (point a), followed by a period of steady growth, then a rapid decline in root growth (point b). This pattern might occur in some perennial crop species (clover; Pearson & Jacobs, 1985), and some annual crops such as wheat (Gibbs & Reid, 1992; Fitter *et al.*, 1996) and leeks (Smit & Zuin, 1996). In such cases, the evaluation of standing root biomass at the end of the growth season would accurately represent the amount of C invested into structural root tissue. However, in some cereals such as wheat, studies have shown that, although there is little root mortality until the end of the life cycle, cortex sloughing might represent a significant loss of biomass (Fig. 2).

Table 1. *Average root life spans for various annual and perennial crop species*

Type	Species	Root cohort	Mean life span (d)	Reference
Annuals	Groundnut (*Arachis hypogaea*)	All roots	24–31	Krauss & Deacon (1994)
	Leeks (*Allium porrum*)	All roots	130	Smit & Zuin (1996)
	Brussels sprouts (*Brassica oleraceae*)	All roots	70	Smit & Zuin (1996)
	Sugar beet (*Beta vulgaris*)	All roots	60–130	Van Noordwijk *et al.* (1994)
	Winter wheat (*Triticum aestivum*)	All roots	>125	Gibbs & Reid (1992)
	Grain sorghum (*Sorghum bicolor*	Spring	42–47	Cheng *et al.* (1990)
		Summer	24–26	Cheng *et al.* (1990)
Perennial herbaceous	Alfalfa (*Medicago sativa*)	22 June–20 July	58–131	Goins & Russelle (1996)
		3–17 Aug	47–92	Goins & Russelle (1996)
	Sugar cane (*Saccharum officinarum*)	All roots	14–90	Ball-Coelho *et al.* (1992)
Perennial woody	Apple (*Malus domesticus*)	All roots	21	Atkinson (1985)
	Apple (*Malus domesticus*)	All roots	14–21	Head (1966)
	Citrus (*Citrus volkameriana*)		16–51	Kosola *et al.* (1995)
	Kiwi (*Actinidia deliciosa*)	All roots	28	Reid *et al.* (1993)
	Trifoliate orange (*Poncirus trifoliata*)	Apr–Dec	90	Eissenstat & Yanai (1997)
	Sour orange (*Citrus aurantium*)		90	Eissenstat & Yanai (1997)
	Cleopatra mandarin (*Citrus reshni*)		116	Eissenstat & Yanai (1997)
	Volkamer lemon (*Citrus volkameriana*)		152	Eissenstat & Yanai (1997)

Fig. 1b probably represents the most typical pattern of root turnover for annual crop species and pasture grasses. In this example, the population of roots is represented by the balance of new root growth and root senescence. Senescence of some fine-root elements is initiated at point b when root growth begins to decline, increases to point c, levels out, and then begins to decline (point d). This general pattern of root turnover has been reported for soybean (Hoogenboom *et al.*, 1987; Huck *et al.*, 1987), cotton (Klepper *et al.*, 1973), sorghum (Cheng *et al.*, 1990; S. G. Pritchard *et al.*, unpublished), and Brussels sprouts (Smit & Zuin, 1996). For many annual crops, the peak of the standing root length occurs before flowering, after which mortality exceeds production (Cheng *et al.*, 1990; Gregory *et al.*, 1996). This decline in root growth and increase in mortality parallels the decrease in C allocation to root systems.

In Fig. 1c the root system maintains a constant rate of growth after point a. Root death occurs as in Fig. 1b. Consequently, standing root biomass would seem to increase in pulses with intervening static periods. This type of root growth would perhaps best characterize tree species that exhibit simultaneous root growth and death (Hendrick & Pregitzer, 1996). Although these theoretical patterns of fine-root initiation and senescence might prove useful for understanding and categorizing plants into different belowground 'functional groups', they are broad generalizations that will describe few species exactly.

It might be important to consider differences in belowground life history strategies when choosing a method to quantify root turnover (for discussions on methodology for quantifying fine-root turnover, see Böhm *et al.* (1977), Cheng *et al.* (1990), Swinnen *et al.* (1995), Bloomfield *et al.* (1996), Majdi (1996), Sinsabaugh *et al.* (1997) and Vogt *et al.* (1998)). Because each procedure has advantages and disadvantages, different methods are appropriate depending on the rooting habits evolved by a given plant species. For example, it might prove unnecessary to spend countless hours harvesting in-growth soil cores or processing thousands of minirhizotron images for an annual plant species that exhibits very little or no root turnover (Fig. 1a). For species in which fine-root production and mortality occur simultaneously (Fig. 1b,c) instead of in asynchronous pulses, the collection of sequential soil cores might provide unreliable results. In cereals such as wheat, it might be more appropriate to examine temporal changes in cortex sloughing because although very little mortality occurs, significant root structural components are lost by means of the programmed cell death of cortex tissue. When an experiment is being designed, it is important to consider the limitations of different methods not only in the context of the specific questions that are

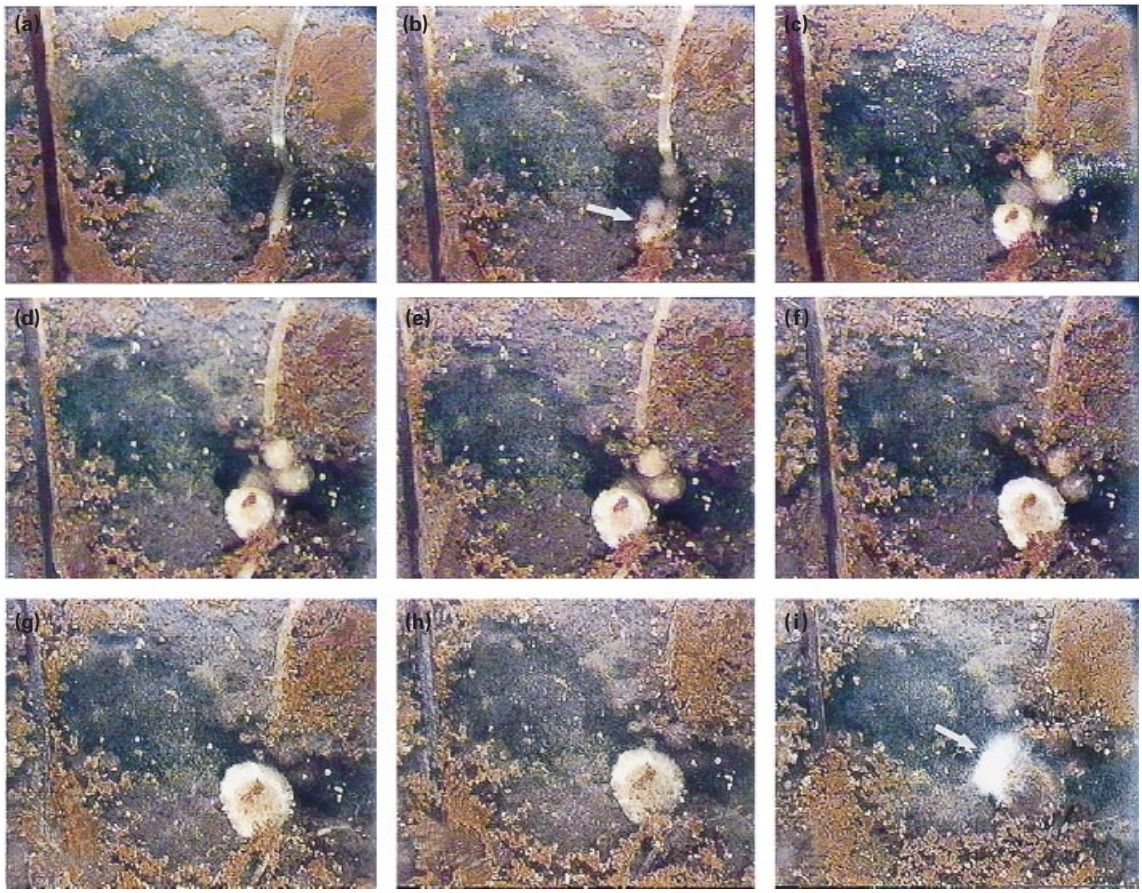

Fig. 3. Sequence of minirhizotron images of soybean collected nine times during the growing season. Each frame represents an area of soil 18 mm × 13.5 mm. (a) 44 d after planting (dap). (b) 57 dap; note the initiation of nodule development (arrowed). (c) 62 dap; (d) 70 dap; (e) 78 dap; (f) 90 dap; (g) 106 dap; (h) 126 dap; (i) 139 dap: the onset of decomposition of the nodule is suggested by the proliferation of fungal hyphae (arrowed). Note that as the nodulated root ages, the association between the root and the soil becomes more intimate, resulting in the establishment of a rhizosheath. These images emphasize the importance of soil structure for root development. For example, the nodules seen here have been initiated and are growing within a soil pore. Analyses of minirhizotron sequences of soybean roots are providing useful information about how environmental change will affect root demography, interactions with symbiotic bacterial N-fixers (i.e. nodule formation), and decomposition.

being asked (Hendrick & Pregitzer, 1996), but also with regard to the rooting habits of the study species.

Mechanistic controls over root senescence

Although very little is known about the average lifespans of crop roots (Smit & Zuin, 1996), existing results suggest a large range of root longevity depending on environmental conditions and taxonomy (Table 1). Identifying the factors and processes that control root death is one of the most significant barriers to understanding the variability in root longevity (Huck *et al*., 1987). Although the mechanistic basis underlying root death is largely unknown, experimental evidence suggests that senescence is controlled by the interplay between genetics, environmental conditions, and damage by soil pathogens (Krauss & Deacon, 1994). Where roots exhibit a determinate growth habit, there might be strict genetic constraints on how many times apical cells divide. Similarly, plasticity of root life spans might be limited in some plants owing to strict genetic limitations (programmed cell death) (Deacon, 1987). The absorptive capacity of fine roots declines with increasing maturity as roots undergo defined developmental and biochemical changes (Figs 2, 3). For example, the suberization of new roots and the loss of root hairs (Fig. 2), which normally occurs within a few weeks, might limit root absorptive capacity, resulting in inefficient resource uptake and eventual senescence (Caldwell, 1977). Although genetics surely has a role in defining root longevity (Marshall & Waring, 1985), environmental conditions are probably also important (Bloomfield *et al*., 1996).

Effects of resource availability on root longevity

The importance of aerial and edaphic environmental conditions in controlling fine-root longevity of crop plants has been shown experimentally. It is thought

that the depletion of resources in soil microsites is the primary stimulus for root mortality. For example, drought seems to induce the mortality of lateral roots in dry soil and causes the production of secondary lateral roots in wetter microsites in some crops (Smucker, 1993). The increase in root longevity with greater soil moisture content seems to be a general phenomenon (Bloomfield *et al*., 1996). Other investigators have suggested that root life spans are controlled by carbohydrate availability (Marshall & Waring, 1985). Goins & Russelle (1996) reported that circumstances that decrease the amount of C fixed by vegetative tissue, or that divert C from roots, increase fine-root mortality in red clover, white clover, and big trefoil. Carbohydrates oxidized in the process of respiration provide the energy to drive biosynthetic and maintenance reactions and transport processes. It is therefore easy to understand how carbohydrate limitations could lead to root death.

If carbohydrate availability and water stress do limit root longevity, then increases in root half-lives might be expected in plants growing in CO_2-enriched environments. As already discussed, increased nonstructural carbohydrate content in roots of plants growing with CO_2 enrichment is common. Furthermore, if senescence of fine roots in dry soil regions is indeed a general phenomenon, then greater soil water availability resulting from decreased water use by plants could also contribute to enhanced root life spans (however, positive effects of reduced leaf-level water use on soil water availability might be counteracted by larger plants). However, the potential positive effects of enhanced soil water and root carbohydrate availability on root longevity could be counteracted by a faster depletion of nutrients in the soil zone surrounding the active root. Currently there is not enough empirical evidence to determine whether root turnover will be enhanced in a future high-[CO_2] world, especially in annual crops.

Effects of soil organisms on root longevity

Damage to roots by belowground herbivores and pathogens might also have a significant role in determining root life spans (Goins & Russelle, 1996). However, Krauss & Deacon (1994) point out that it is difficult to determine whether fine-root death is genetically programmed, is a consequence of environmental stress, or is initiated by pathogens. Because senescing roots are often immediately colonized by microbes (Fig. 3i), it is difficult to determine whether senescence leads to pathogen infection or whether pathogen infection leads to senescence.

Growth in elevated [CO_2] might increase the amount, and change the quality, of aboveground and belowground plant litter and exudates that enter the soil. These changes in soil biochemistry could result in shifts in the populations of soil microbes and fauna that have important roles in determining root longevity (Díaz, 1996). Furthermore, increased root turnover in plants grown in elevated [CO_2] would provide a rich source of nutrients for colonization by soil organisms (Smucker, 1993), possibly leading to an increased buildup of pathogens in the root zone (Fig. 3). Klironomos *et al*. (1996) found that exposure of plants to elevated [CO_2] resulted in a shift in the balance between mycorrhizal and non-mycorrhizal fungi and bacteria. They later reported that exposure to elevated [CO_2] resulted in a stimulation of a mycorrhizal-based soil food web when soil N was limiting, and a stimulation of the opportunistic–saprobic/pathogenic-fungus-based food web when N was nonlimiting (Klironomos *et al*., 1997). The increase in pathogenic fungi in high N could result in more root disease and higher mortality. However, it is still not clear how changes in plant exudation and turnover will affect both the quantitative and qualitative characteristics of soil microbial populations (Gorissen, 1996), and how changes in biomass and species composition of soil organisms will then feed back on root demographics.

ELEVATED [CO_2] AND CROP FINE ROOTS: EXISTING DATA

Growth in elevated [CO_2] has been shown to increase fine-root biomass in FACE-grown cotton (Rogers *et al*., 1992b) and wheat (Wechsung *et al*., 1995). In the wheat experiment, roots from FACE grew earlier and more extensively into the inter-row space. In addition, the decline in total root biomass after anthesis was not affected by the CO_2 treatment. At a finer scale, wheat root biomass in the upper 15 cm remained higher until harvest in elevated [CO_2], whereas at lower soil depths (15–100 cm), root growth decreased more rapidly. Jongen *et al*. (1995) reported increases in root in-growth (production) of perennial ryegrass and clover grown in elevated [CO_2]. They observed a maximum increase in root production from June to August and from August to November in perennial ryegrass and clover, respectively. To our knowledge, there is only one published report on the effects of elevated [CO_2] on root turnover in a crop species. Fitter *et al*. (1996), using minirhizotrons, found no changes in root turnover in wheat grown in elevated [CO_2] because wheat undergoes little or no mortality until all roots die synchronously at the end of the life cycle, as in Fig. 1a and illustrated in Fig. 2. However, they did report that spatial and temporal patterns of root deployment were altered in wheat grown in dry soil; root development was enhanced between 3 and 5 wk in surface layers (10–15 cm) and was slowed down between 5 and 8 wk in deeper layers (80–85 cm) in wheat grown in elevated [CO_2].

AGRICULTURAL MANAGEMENT AND FINE ROOTS

Tillage

Some form of conservation tillage is expected to be adopted on 60–80% of agricultural land in the USA by the year 2010 (Lee *et al.*, 1993). The conversion to more sustainable agricultural practices will increase soil C sequestration, decrease erosion, change soil/plant water relations, and affect the overall growth and development of crop roots (Turman *et al.*, 1995). In fact, the magnitude of the impact of agricultural management practices on fine-root production and mortality, and the resultant transfer of C to soil, might overshadow any effects of elevated [CO_2] on these processes (Canadell *et al.*, 1996). Using the CENTURY model to determine the interactions of temperature, precipitation, elevated [CO_2], and management practices, Paustian *et al.* (1996) found that agricultural management practices were more important than climate change and elevated [CO_2] in controlling amounts of soil C. Therefore, interactive effects of agricultural management practices with increasing global [CO_2] must represent the main thrust of research concerning the impact of future global change on agricultural.

Tillage practices affect soil moisture retention, biomass, and species composition of soil organisms, C and N dynamics, soil micro-aggregate structure, and soil bulk density (Cheng *et al.*, 1990). These differences in soils often contribute to altered root growth in crops grown without tillage compared with those grown under conventional tillage (Goins & Russelle, 1996). Roots of crop plants grown without tillage typically concentrate a greater proportion of their root system at shallow soil depths than do root systems in conventional tillage (Whiteley & Dexter, 1982; Cheng *et al.*, 1990; Rasse & Smucker, 1998), perhaps because of greater surface soil moisture availability and lower soil bulk density without tillage. Although a substantial quantity of data indicate that root spatial distributions are significantly affected by tillage practices, it is still unclear whether root temporal distribution or demography differ consistently in conventional compared with sustainable systems. Swinnen *et al.* (1995) found that decay and turnover in barley roots were higher in conventional agricultural systems than in the integrated one, but were unchanged in wheat. In another study, sugar beet grown with minimum tillage had lower fine-root production than in the conventional cropping system, whereas fine-root production of wheat was unchanged (Van Noordwijk *et al.*, 1994).

The adoption of conservation management practices on large areas of cropland during the next 30 years could sequester all the CO_2 emitted from agriculture and up to 1% of fossil fuel emissions in the USA (Lal, 1999; Schlesinger, 1999). The capacity of agricultural soils to sequester C in a future higher-[CO_2] world will therefore be a function of how extensively and efficiently we are able to implement conservation management practices in conjunction with the degree to which crop-mediated flow of C into, within, and out of soils will be affected. In view of the current lack of data, and the trend toward the increased adoption of conservation tillage practices, the influence of agricultural management practices on crop root deployment in CO_2-enriched atmospheres clearly deserves study.

Soil structure

Soil is composed of micro-aggregates (pedosomes) that are bound together into a hierarchy of sizes by fungal hyphae and fine roots of plants (Harris, 1999). Micro-aggregates, inhabited by interacting populations of bacteria and fungi, are sites of intense biological activity that function in the fixation of N, ammonification, nitrification, and denitrification (Harris, 1999). Micro-aggregates might represent the fundamental organizational unit of soils in the same way that cells are the fundamental units within living organisms. Fine roots influence these structures by exerting pressures that contribute to aggregation, causing stresses and strains through localized soil drying, supplying rhizodeposition, which either directly or indirectly stimulates aggregation, and serving as a source of organic matter (Jastrow *et al.*, 1998). High root-length densities resulting from the proliferation of very fine roots can also physically limit the development of larger macro-aggregates. The maintenance and size distribution of soil aggregates therefore depend on both the quantity and quality of standing root mass, root exudates, and root necromass. Fig. 4 presents a conceptual model that illustrates the qualitative effects of greater belowground C allocation on fine-root proliferation, soil resource availability, soil microbial function, root mortality, and soil structure. A better understanding of the influence of plant biology on soil biology will emerge as each link within this model receives further study. It is likely that changes in rooting characteristics of plants growing in CO_2-enriched environments will contribute to either improved or degraded soil structure. Changes in soil structure can then either positively or negatively feed back on plant root structure and function (Figs 3, 4).

The effects of elevated [CO_2] on soil structure, mediated by changes in plant root structure and function, are largely unexplored. We are aware of only one published study examining the linkage of atmosphere with soil. Rillig *et al.* (1999) recently showed that exposure of two annual grassland ecosystems to long-term elevated [CO_2] induced

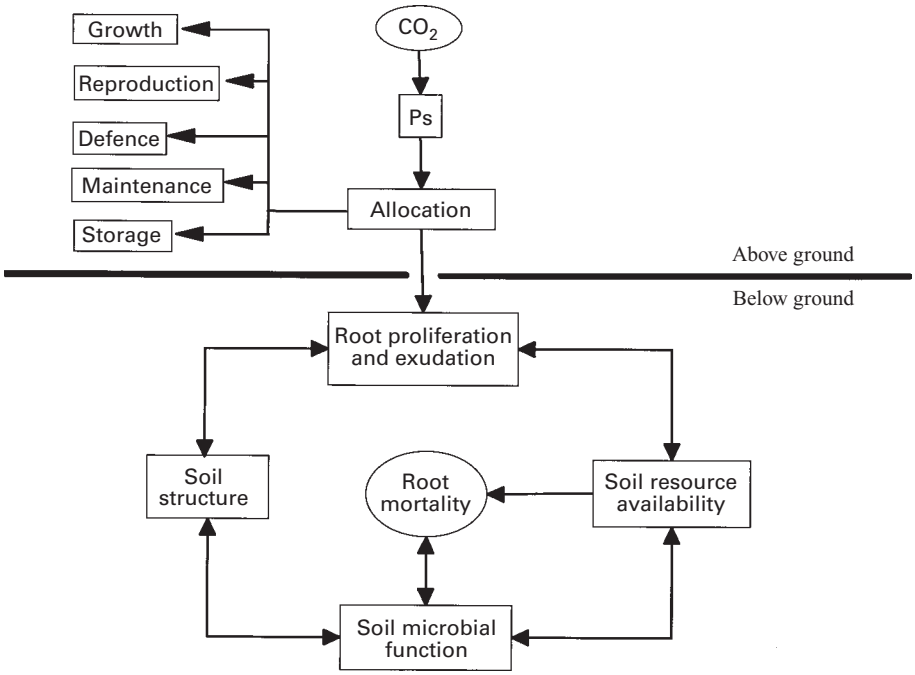

Fig. 4. Conceptual model illustrating the interactions and feedbacks among C allocation, root proliferation, soil resource availability, soil microbial function, root mortality, and soil structure. Ps, photosynthesis.

changes in the water stability and size distribution of soil aggregates. They attributed these changes to an increase in glomalin concentrations in the soil under CO_2 enrichment. Glomalin, a glycoprotein produced by hyphae of mycorrhizal fungi, has been shown to be tightly correlated with the aggregate stability of soils (Rillig *et al.*, 1999). So, presumably, exposure to elevated [CO_2] led to increased C to roots, which stimulated mycorrhizae, which in turn produced more glomalin, leading to notable changes in soil structure.

CONCLUSIONS

Crop roots in future higher-[CO_2] environments will develop differently because increased root C availability will stimulate, perhaps to differing extents, cell division and expansion within root apical meristems. However, the stimulation of primary roots in some crop plants might be inherently limited by a determinate growth habit. Most changes in root architecture will therefore involve activation of more pericycle initials, leading to greater lateral root stimulation and more extensive root branching. Greater root branching will lead to larger, but perhaps less efficient, root systems. Data also suggest that most stimulation of crop roots will occur at shallow soil depths. More shallow rooting will have consequences not only for water and nutrient uptake but also for soil C and N dynamics.

Specific root activity (i.e. respiration and nutrient uptake) often decreases in crop plants growing in elevated [CO_2], even though plants allocate C preferentially below ground. The inability of crops to acquire nutrients to keep pace with increased C assimilation in CO_2-enriched environments will probably act as a negative feedback on productivity and yield. This negative feedback will lead to shifting patterns of C allocation to root systems throughout life cycles of plants as they equilibrate structurally and functionally to maximize the balance between aerial growth and resource availability with belowground growth and resource availability. The use of techniques such as ^{14}C and ^{13}C labeling in conjunction with minirhizotrons will facilitate a more complete understanding of the temporal and spatial patterns of belowground C allocation, root growth, and resultant patterns of soil C sequestration.

Little information is available about the effects of elevated [CO_2] on the trade-offs associated with maintaining old roots in comparison with building new ones. In light of the current, but limited, understanding of the controls on root longevity, it is unlikely that there will be any appreciable changes in life spans of finer root elements. Although root longevity is unlikely to change in crops as a direct result of increased root C availability, life spans might be affected indirectly through shifts in soil moisture and nutrient availability, by changes in biological activity, or as a result of altered soil structure. Although greater root turnover has been reported for forest and grassland ecosystems, there are still insufficient empirical data to either support or refute the possibility of increased root turnover in crops, especially annual species.

Although the temporal and spatial deployment of fine roots has been recognized as one of the most important and the least understood components of belowground C cycling, and perhaps the entire global C cycle (Torn *et al.*, 1997), few data exist on

the effects of elevated [CO_2] on these processes, especially in crop plants. To create an accurate global model incorporating water and nutrient uptake, and C sequestration, we must first understand how increasing [CO_2] will affect the absorptive surface area of live fine roots, their spatial distribution in the soil, and their demography (Jackson *et al*., 1997).

RECOMMENDATIONS

We suggest that the following be taken into consideration in future research on the effects of elevated [CO_2] on crop root development.

- A better understanding of the cellular (cell division and expansion) and tissue-level (lateral root initiation) events contributing to root developmental shifts in CO_2-enriched environments will help to link atmospheric C levels, plant C allocation, and root growth mechanisms. Controlled laboratory experiments, using *Arabidopsis* mutants, to determine how normal root developmental events are changed by growth in elevated [CO_2], as proposed by Crookshanks *et al*. (1998), should prove particularly useful in this regard.
- Studies on root function should be designed to take into consideration shifting patterns of C allocation over the life cycle of the study plant. A knowledge of temporal shifts in C allocation below ground will prove vital for characterizing the accompanying shifts in root production and mortality. This will contribute to a more thorough understanding of the link between plant, soil, and atmosphere.
- Data are required to characterize the influence of elevated [CO_2] on root demography in crops, especially annual species. Focused study of root turnover and root longevity in crops exhibiting different rooting habits (life histories) will be important for understanding C flow into, and sequestration within, agricultural soils.
- Because of the widespread adoption of sustainable agricultural systems, the interactive effects of elevated [CO_2] with agricultural management practices deserve study.
- The influence of elevated atmospheric [CO_2] on plant-root-mediated changes in soil structure and ecology should receive more attention. Furthermore, potential feedback from any resultant physical and biological changes in soil on root growth, demography, and function should be explored.

ACKNOWLEDGEMENTS

We thank T. Rost, N. Kerk, C. M. Peterson, and P. Barlow for helpful suggestions, and M. A. Davis and G. B. Runion for critical reviews of this manuscript. This work is supported by Interagency Agreement no. DE-AI05-95ER62088 from the US Department of Energy, Environmental Sciences Division. Any opinions, findings, and conclusions or recommendations expressed in this publication are those of the authors and do not necessarily reflect the views of the US Department of Energy or the US Environmental Protection Agency.

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